Elements of metacommunity structure of diatoms and macroinvertebrates within stream networks differing in environmental heterogeneity

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Running Head: Metacommunity Structure of Chinese Streams

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ABSTRACT

Aim Idealized metacommunity structures (i.e. checkerboard, random, quasi-structures, nested, Clementsian, Gleasonian, and evenly spaced) have recently gained increasing attention, but their relationships with environmental heterogeneity and how they vary with organism groups remain poorly understood. Here we tested two main hypotheses: (1) gradient-driven patterns (Clementsian and Gleasonian) occur frequently in heterogeneous environments, and (2) small organisms (here, diatoms) are more likely to exhibit gradient-driven patterns than large organisms (here, macroinvertebrates).

Location Streams in three regions in China.

Taxon Diatoms and macroinvertebrates

Methods The stream diatom and macroinvertebrate data, as well as the environmental data collected from the same set of sites were used to examine the idealized metacommunity structures via the elements of the metacommunity structure (EMS; coherence, turnover, and boundary clumping) analysis in three regions. We extended the traditional EMS approach by ordering sites along known environmental gradients.

Results We found that Clementsian structure with high degrees of coherence and turnover, and significantly positive clumping was typically observed in the high-heterogeneity regions, whereas randomness was prevalent in the low-heterogeneity region. Macroinvertebrates exhibited clearer Clementsian structures compared with diatoms, while diatoms showed more randomness compared with macroinvertebrates, indicating a stronger role of environmental filtering for macroinvertebrates than diatoms. In most cases, the results of the more novel EMS approach differed from the results of the traditional EMS technique.

Main conclusions Our results suggested that the occurrence of different metacommunity structures may be related with the degree of regional environmental heterogeneity. However, diatom metacommunities were more random than those of macroinvertebrate, and such an unexpected result may result from different dispersal abilities between the two organism groups. In addition, we found that the novel EMS approach increased power in discerning metacommunity structure in comparison to the traditional EMS technique.

Key words: Clementsian, Random, Environmental heterogeneity, Aquatic organisms, China, Idealized metacommunity structure

INTRODUCTION

The metacommunity concept, a set of local communities connected through species dispersal, is a useful framework to evaluate the variation in community composition in space (Leibold et al., 2004; Logue, Mouquet, Peter, Hillebrand, & Grp, 2011). Within the metacommunity framework, spatial patterns of species distribution can be described as one of 10 possible structures (Leibold & Mikkelson, 2002; Presley, Higgins, & Willig, 2010). Nested structure occurs when the species-poor sites represent subsets of species-rich sites (Patterson & Atmar, 1986). In contrast, in Clementsian, Gleasonian, and evenly spaced structures, the majority of communities replace each other along the latent environmental gradient (Bried & Siepielski, 2018). These structures associated with high turnover are referred to as gradient-driven patterns and potentially indicate the important role of environmental filtering along the underlying gradient (Meynard et al., 2013; Presley et al., 2010). Yet, the theoretical underpinnings of these three patterns are fundamentally different. For example, Clementsian gradients consist of discrete communities that replace each other as a group (Clements, 1916), while Gleasonian gradients suggest individualistic responses of taxa to the environment that yield a continuum of gradually changing composition without the formation of discrete assemblages (Gleason, 1926). In random structure, species respond independently to each other and differently to multiple environmental gradients across space, while checkerboard structure comprises pairs of mutually exclusive species across space (Diamond, 1975). Finally, quasi-structures (Q-structures) are characterized by the same characteristics as their associated idealized structures but with weaker underlying structuring processes (Erős, Takács, Specziár, Schmera, & Sály, 2017; Presley et al., 2010).

Idealized metacommunity structures may vary with environmental heterogeneity. Biological communities are currently threatened by the loss of environmental heterogeneity caused by anthropogenic modifications and climate warming, which may lead to community homogenization and metacommunity structure simplification (Colossi Brustolin et al., 2019; Wojciechowski, Heino, Bini, & Padial, 2017). Hence, there is considerable urgency to understand the effect of environmental heterogeneity on metacommunity structure. In highly heterogeneous environments, evidence suggests that the metacommunity under investigation would follow a strong turnover pattern such as Clementsian structure (Bried & Siepielski, 2018; Gascón et al., 2016; Erős et al., 2017) and Gleasonian structure (Tonkin et al., 2017). However, when environmental heterogeneity decreases but remains moderate, different outcomes may emerge, and a metacommunity would display a structure with weaker turnover such as quasi-structures (Erős et al., 2017). This is because less heterogeneous conditions in a region potentially offer less niche opportunities for the species to occur in suitable habitats and typically incorporate species with narrow ranges of environmental optima (Heino, Melo, & Bini, 2015), leading to low species turnover along the environmental gradient (Erős et al., 2017). Finally, in regions with low environmental heterogeneity, environmental gradients may not be important drivers of metacommunity structure, likely creating ecologically non-meaningful patterns such as randomness (Bried & Siepielski, 2018).

Idealized metacommunity structures could also differ among organismal groups with different traits (Heino, Soininen, Alahuhta, Lappalainen, & Virtanen, 2015). For example, stream diatoms and

119 macroinvertebrates exhibit differences in body size, dispersal ability, and dispersal mode (De Bie et
120 al., 2012), which would therefore cause them to respond differently to the environmental gradients.
121 Diatoms are small and highly abundant unicellular organisms and perhaps better passive dispersers
122 than larger-sized macroinvertebrates in general (Astorga et al., 2012; Heino, Grönroos, Soininen,
123 Virtanen, & Muotka, 2012). They may thus be better able to track environmental variation quickly
124 along the environmental gradient and are expected to show stronger degree of environmental
125 filtering than macroinvertebrates. Moreover, compared with diatoms, macroinvertebrates can also
126 actively select suitable habitats via dispersal (Farjalla et al., 2012). Comparison of diatoms and
127 macroinvertebrates may thus provide important insights into how dispersal mode and environmental
128 heterogeneity interact to determine metacommunity structure (Heino, 2013). In addition, the
129 environmental gradient driving species composition could also differ between two groups. Previous
130 studies suggested that both physical and chemical variables are key factors influencing diatoms, while
131 physical variables typically are the most important factors influencing macroinvertebrates (Heino et
132 al., 2012; Heino, Nokela, et al., 2015). However, based on earlier studies, there appear to be no clear
133 differences in idealized metacommunity structures between diatoms and macroinvertebrates (Heino,
134 Nokela, et al., 2015; Heino, Soininen et al., 2015). A potential problem with these earlier studies is
135 that idealized metacommunity structures have been evaluated by the traditional EMS approach
136 (Leibold & Mikkelson, 2002), which fails to discern the observed structures and may obscure the
137 potential influence of the environment on such structures (Dallas, Kramer, Zokan, & Drake, 2016;
138 Schmera, Podani, Botta-Dukát, & Erős, 2018). However, a novel EMS approach of ordering sites by
139 known environmental gradients represents a potentially powerful method to overcome such
140 problems (Dallas et al., 2016; Schmera et al., 2018). Thus, it is necessary to use the novel EMS
141 approach to compare metacommunity structures of diatoms and macroinvertebrates, and using this
142 approach may lead to different conclusions (Dallas et al., 2016).
143 Streams are suitable model systems for examining the effects of environmental heterogeneity on
144 metacommunity structure because they range from relatively environmentally homogeneous to
145 extremely heterogeneous systems (Bini, Landeiro, Padial, Siqueira, & Heino, 2014). Idealized
146 metacommunity structures have received well-deserved attention in stream systems recently (Erős
147 et al., 2017; Heino, Nokela, et al., 2015; Tonkin et al., 2017). Here, we investigated the EMS of stream
148 diatoms and macroinvertebrates from the same set of sites in three regions in China (Fig. 1). These
149 regions show high regional variation of environmental heterogeneity because they located at
150 different climatic zones and experienced different degrees of urbanization (Chen et al., 2019; Ding et
151 al., 2017; Wang et al., 2012). Stream communities across a set of sites within a region were defined
152 here as a metacommunity. Our main questions were: (1) does idealized metacommunity structure
153 vary across three regions that exhibit different levels of environmental heterogeneity? (2) Do
154 idealized metacommunity structures differ between diatoms and macroinvertebrates? We
155 hypothesized first that (**H_1**) turnover-based patterns (Clementsian or Gleasonian) should be stronger
156 in the region with greater environmental heterogeneity, whereas randomness or quasi-structures
157 should be more likely in the region with lower environmental heterogeneity. Given that habitat
158 associations could be stronger for diatoms than macroinvertebrates, we hypothesized that **(H_2)**

diatom metacommunities are more likely to exhibit turnover-driven patterns (Clementsian or Gleasonian) than those of macroinvertebrates, particularly in the region with higher environmental heterogeneity. In addition, compared with diatoms, some groups of macroinvertebrates can only be identified to higher taxonomic resolution (Heino et al., 2012). Such a limitation is especially pressing in Asian research due to the lack of comprehensive identification keys for macroinvertebrates (Morse et al., 1994). The difference in identification efforts would potentially cause macroinvertebrates and diatoms to exhibit different EMS patterns. However, as only very few studies have examined the influence of taxonomic resolution on metacommunity structure (Martin, Adamowicz, & Cottenie, 2016; Verleyen et al., 2009), we examined if EMS patterns varied across taxonomic levels in both diatoms and macroinvertebrates. We hypothesized that (**H_3**) turnover-driven patterns (Clementsian or Gleasonian) would be more common at lower taxonomic levels due to a higher likelihood of taxonomic replacements among communities (Tonkin et al., 2017). We considered these three specific hypotheses only for Clementsian, Gleasonian, random, and quasi-structure patterns, because nested, evenly spaced, and checkerboard metacommunities tend to occur rarely in freshwater systems (Heino, Soininen et al., 2015; Presley, Mello, & Willig, 2019).

MATERIALS AND METHODS

Study area

In this study, we used a unique data set containing three geographically distant regions: the upper section of the Mekong River (MKR) in Xishuangbanna Prefecture, the middle section of the Qiantang River (QTR) in Zhejiang Province, and the Irtysh River (ITR) in Xijiang autonomous region in China (Fig. 1). The study regions are evidently different in natural climatic conditions and human land use characteristics (Fig. 1; Table 1) (Chen et al., 2019; Ding et al., 2017; Wang et al., 2012), thus showing notable differences in among-region environmental heterogeneity. MKR is a tropical rain forest area characterised by a tropical monsoon climate (Ding et al., 2017). QTR and ITR are characterised by a subtropical monsoon climate (Wang et al., 2012) and a temperate arid climate (Chen et al., 2019), respectively. In recent years, MKR and QTR have undergone a significant land use change such as a decline in forest cover (Ding et al., 2017; Wang et al., 2012). Land use in ITR is dominated by livestock grazing, but much of the upper basin supports natural forests (Chen et al., 2019). In total, 115 (33 in ITR, 37 in MKR, 43 in QTR) sampling sites were surveyed mostly in streams (1^{st} to 4^{th} orders) in the three regions.

Biological sampling

Benthic diatoms and macroinvertebrates were collected simultaneously from a 100 m-long reach at each sampling site. We collected diatoms from nine transects at each site. Diatoms were scraped off from one coarse substrate particle from a defined area (10.17 cm^2) with a toothbrush and an area delimiter (PVC tube) at each transect. We washed and combined the nine subsamples into a single composite sample, and added distilled water to a constant volume of 500 ml. We then extracted 50 ml out of the 500 ml to a specimen bottle for taxonomic analysis and preserved the sample by adding two ml of 10% formalin. In the laboratory, a total of 500 frustules per sample were identified and counted with a light microscope (Olympus BX41TF) at 1000× magnification. All diatom individuals were

identified to the species level (Krammer, 2003; Krammer & Lange-Bertalot, 1986, 1988,1991a, 1991b).

We collected macroinvertebrates using a Surber-net (30 × 30 cm, 250 μm mesh size) from three riffles and two pools with a total of 0.45 m^2 sampling area (Chen et al., 2019). All Surber net samples were combined into one composite sample and preserved in 10% buffered formalin. In the laboratory, macroinvertebrates were sorted, counted and identified to the lowest practical taxonomic level, in most case to genus (> 85% of taxa) (Morse et al., 1994).

Environmental variables

We measured physical habitat and water chemical variables at each site. We used a METTLER TOLEDO meter (model SG23, Mettler) to measure water temperature (WT), pH, total dissolved solids (TDS) and conductivity (Cond) in situ. We used a portable meter HI93752 (Hanna, Italy) to measure calcium (Ca^{2+}) and magnesium (Mg^{2+}) concentrations. We measured channel width and water depth across five transects at each site. We also estimated the percentages of different substrate categories (i.e. % sands, % gravels, % cobbles, and % boulders) (Kondolf, 1997; Wolman, 1954). Elevation was documented with a Garmin eTrex. Prior to the field measurements and biotic sampling, we collected one 500 ml water sample at each riffle and stored them in a portable refrigerator at < 4°C. In the laboratory, we analysed these samples for total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_4-N), phosphate (PO_4-P) contents and determined the potassium permanganate index (COD_{Mn}). We followed Chen, Hughes, & Wang, (2015) to delineate the watershed boundaries for each site using the Multi-Watershed Delineation Tool and ArcGIS 9.3 software (Esri, Redlands, CA, USA) with 30-m resolution digital elevation models provided by the Chinese Academy of Sciences (http://www.cnic.cn/). We then included a digital land-use raster layer provided by GLOBELAND30 (http://www.globallandcover.com/) to estimate the percentages of three land-use types (i.e. % forest, % farmland, and % urban) within each watershed. We also used 19 bioclimatic variables available in the WorldClim database (http://www.worldclim.org/), at a resolution of 2.5' (～25 km^2).

To account for collinearity among environmental variables and avoid overfitting in the following EMS sites-based ordination analyses, we selected 16 environmental variables based on among-variable correlations (Pearson $r < 0.7$) using the 'corr.test' function in the psych package (Revelle, 2018). These variables were: WT, pH, TDS, Ca^{2+}, Mg^{2+}, % sands, % gravels, % cobbles, % boulders, elevation, TN, TP, NH_4-N, COD_{Mn}, % forest, mean diurnal range (BIO2) (Appendix S1). Prior to EMS analysis, we transformed all these selected environmental variables (except pH) using log or centred log ratio (i.e. % forest and substrata data) transformations.

Environmental heterogeneity

We used an analysis of homogeneity of group dispersions (PERMDISP; Anderson, 2006) to test the possible differences in the degree of environmental heterogeneity among the three regions. In our case, we calculated mean dispersions across streams within a region (mean distances of sites to group (a region) centroid) as a measure of environmental variability. Prior to PERMDISP analysis, we standardized each environmental variable to mean = 0 and SD = 1 using the 'scale' function in R. We used ANOVA F-statistic to compare within-group distances to each group centroid and tested the significance of the differences among groups with 1000 permutations. We conducted the PERMDISP analysis using the 'betadisper' function in vegan R package (Oksanen et al., 2013).

Elements of metacommunity structure

We used the elements of metacommunity structure (EMS) analysis to determine the metacommunity structures of diatoms and macroinvertebrates. The EMS interpretation is based on three metrics: coherence, turnover and boundary clumping, which were compared to a null distribution from the fixed-proportional (R1) null model (Presley et al., 2010) at a significance level $\alpha = 0.05$ based on 999 simulations. Coherence reflects the degree to which species respond to the same environmental gradient; turnover represents how species composition changes among localities along the gradient; and boundary clumping measures the degree to which species range boundaries occur together (Leibold & Mikkelson, 2002; Presley et al., 2010). Prior to calculating the three metrics, sites-by-taxa matrix (presence-absence data) is ordinated via reciprocal averaging (RA, Hill, 1973), which maximizes the positioning of sites with similar taxa compositions and the positioning of taxa with similar ranges. Additionally, with the purpose of arranging diatom and macroinvertebrate communities (i.e. the "site" of matrix) by observed environmental gradients, we sorted sites by the selected environmental variable one by one following a recent EMS study (Dallas et al., 2016). Sites were also ordered by overall environmental gradients obtained from the first axis of principal component analysis (PCA1) on the 16 environmental variables. Therefore, each matrix was analysed 18 times resulting in 18 different EMS results per region and per taxonomic group. We used a standardized effect size (Z) to facilitate comparisons among the regions (Heino, Soininen et al., 2015; Gurevitch, Morrow, Wallace, & Walsh, 1992; Gotelli & McCabe, 2002). We calculated Z as: $Z = (Obs - Mean)/SD$, where 'Obs' is the observed index value (for coherence or turnover), and 'Mean' and 'SD' are the average and standard deviation of null model simulations. Additionally, Z-scores of coherence and turnover can be used to quantify variation in metacommunity classifications within a continuous space because using this continuous space may offer a novel way to examine the influence of environmental factors on metacommunity structure (Dallas et al., 2016; Heino, Soininen et al., 2015). See Appendix S2 for more detailed description on how these EMS metrics are computed and which idealized pattern best fits the metacommunity data.

We used the R (R Core Team, 2016) package Metacom (Dallas, 2014), which relies on functions from the vegan package (Oksanen et al., 2013), using R version 3.2.2 (R Core Team, 2016) to examine the EMS. Prior to all analyses, we removed rare species occurring at < 5% of the sites to reduce their potentially disproportionate effects on the results (Presley, Higgins, Lopez-Gonzalez, & Stevens, 2009). We also performed EMS analyses on data including all species, but overly long computation time with no results often occurred, probably because of relative low number of sites and high number of taxa (e.g. n = 184 for macroinvertebrates in the MKR region). Finally, to examine the influence of taxonomic resolution on the metacommunity structures, we ran EMS analyses using species, genus, and family level data for diatoms, and genus and family level data for macroinvertebrates. In total, we had 90 matrices (18 ordinations $\times$ (3 taxonomic levels in diatoms + 2 taxonomic levels in macroinvertebrates)) for the analyses in each region. To remove the potential influences from variable sample size, we standardized (randomly selected using the 'sample' function in R) the number of stream sites in the MKR and QTR regions to 33 (we chose 33 since this was the maximum number of sites available in ITR).

Given that each sites-by-taxa matrix in each region needed to be analysed more than eighty times (n = 90) in the EMS analysis, we thus conducted the standardizing exercise only one time to avoid a huge number of EMS analysis. The random subset data sets were retained the original spatial extent of the entire data sets (random subset data: 168 km in MKR, 201 km in QTR; whole data: 168 km in MKR, 206 km in QTR). We conducted all analyses using only the randomly selected sites in the MKR and QTR regions and the sampled sites in the ITR region (Fig. 1).

RESULTS

Environmental heterogeneity

Environmental heterogeneity differed among the three regions based on PERMDISP analysis ($F_{2, 96}$ = 5.73, P = 0.004), with the QTR region showing the highest environmental heterogeneity (mean Euclidean distance to group centroid ± Standard Error: 3.94 ± 0.41), followed by the MKR region (3.15 ± 0.17) and the ITR region (2.64 ± 0.15). In addition, a PCA ordination plot (Appendix S3) showed that the sites in the QTR region were much more dispersed than those in the MKR and ITR region.

Metacommunity structures

In total, six idealized metacommunity structures were found in EMS analysis (Table S4.1). We found that random (n = 108) and Clementsian (n = 95) structures were the most common, followed by Q-Clementsian (n = 36), Q-Nested (n = 22), Gleasonian (n = 4), and Q-Gleasonian (n = 5) types (Table S4.1).

In most cases, the same metacommunity ordered along the traditional RA ordination gradient and environmental gradients exhibited different results (Table S4.2, S4.3, and S4.4). For example, in the MKR and QTR regions, the diatom metacommunities ordered based on site-by-family and site-by-genus information showed non-significant coherence, indicating a random structure (Table S4.2 and S4.3). However, when sites were ordered based on TDS, Ca^{2+} and BIO2, the metacommunities showed significant positive coherence, indicating a non-random structure (e.g. Clementsian, Q-Clementsian, and Gleasonian structures, Table S4.2 and S4.3).

Variation in metacommunity structures among regions

The EMS analysis revealed considerable variation in metacommunity structures among the three regions. Generally, random structure was more common in the ITR region with the lowest environmental heterogeneity, while Clementsian pattern was more common in the QTR region with the highest environmental heterogeneity (Fig. 2). Moreover, the degree of coherence and turnover differed clearly among three regions, with the QTR region showing the highest coherence and turnover, followed by the MKR region and the ITR region (Fig. 2). Thus, these results supported hypothesis $\mathbf{H_1}$.

Differences in metacommunity structures between organism groups

Considerable variation in metacommunity structure was also evident between two organism groups. Macroinvertebrates showed clearer Clementsian structures than diatoms in the QTR and MKR regions, while diatoms fitted more clearly random distributions compared with macroinvertebrates (Table S4.1). These results suggested that diatoms are more randomly distributed along the environmental gradient than macroinvertebrates in the QTR and MKR regions, thus disagreeing with hypothesis $\mathbf{H_2}$.

Variation in metacommunity structures among taxonomic levels

We found some differences in diatom metacommunity structures among taxonomic levels. The numbers of randomness were higher at family and genus taxonomic level in each region, while the numbers of Clementsian-type turnover patterns were more common at species taxonomic level in the QTR and MKR regions (Table S4.1), partly agreeing with hypothesis **H_3**. Evidence for Gleasonian and Q-Gleasonian appeared only at higher taxonomic levels (Table S4.1).

DISCUSSION

In this study, the hypothesis that idealized metacommunity structures would differ among the three regions with varying environmental heterogeneity was supported. We found that higher environmental heterogeneity did promote strong species responses along certain environmental gradients, resulting in clear turnover patterns (e.g. Clementsian structure). However, our specific hypotheses regarding the notable differences in metacommunity structure between two aquatic organism groups and among taxonomic levels were not supported or were only partially supported, respectively. We propose that the extended EMS approach used in this study provides more useful information for examining the effects of the environment on metacommunity structure, and we thus strongly recommend its use in the context of the EMS framework.

Variation in metacommunity structure among regions

Our results revealed considerable variation in the metacommunity structure of diatoms and macroinvertebrates among the three regions, likely because of the significant differences in within-region environmental heterogeneity among the regions. Metacommunity structure characterized by the Clementsian type with high degree of turnover and coherence in QTR emerged because these streams spanned a higher degree of environmental variability and covered more contrasting habitat conditions (Appendix S4). Thus, with such high environmental heterogeneity, ecologically different species should be able to inhabit different habitat conditions (Gascón et al., 2016). By contrast, random structure along environmental gradients frequently emerged in the low-heterogeneity ITR region, possibly because environmental heterogeneity was too low to strongly influence metacommunity structuring (Erős et al., 2017). Our results have implications for stream conservation. For example, given that the clumps of co-occurring species were distributed in space (Clementsian type) in the OTR region, effective conservation planning in highly heterogeneous regions should consider each area being composed of groups of species with discrete boundaries and similar responses to environment to maintain regional biodiversity. However, in the ITR region for diatoms, presence of many Quasi-Nested (Fig. 2) structures indicate that taxa loss may exist (Presley et al., 2010). Thus, conservation efforts in the ITR region for diatoms should maintain taxa-rich streams to prevent biodiversity loss.

In contrast to our results, Heino, Nokela, et al. (2015) found no evidence of a clearer fit with the turnover-driven patterns in the region with higher environmental heterogeneity. A reason for such differences between these results may stem from differences in the ways used to analyse metacommunity structure. Unlike Heino, Nokela, et al. (2015), we used the extended EMS analysis (i.e. ordering sites not only by the traditional RA site scores, but also by the measured environmental gradients), which may be a more informative approach to investigate how differences in environmental

conditions within and among regions could affect the idealized metacommunity structures (see also Schmera et al., 2018). For example, the diatom metacommunity had an ecologically non-meaningful pattern (i.e. randomness) in the MKR region when the site-by-genus matrix was ordered by traditional ordination (i.e. by RA scores) (Table S4.3). However, when site-by-genus matrix was ordered by novel approaches, such as by mean diurnal range (BIO2) gradients, the diatom metacommunity resembled Gleasonian structure (Table S4. 3). This significant structure suggests that diatom taxa replaced one another in a continuum of communities across the BIO2 gradient in the MKR region. Moreover, BIO2 was weakly (rho = -0.25, df = 31, p = 0.15) related to the RA score. Such an example suggests that the traditional ordination-based approach likely masked the influence of individual environmental gradients. Consequently, ordering of sites by known environmental gradients in the EMS framework may help us to better detect the influence of environmental conditions on metacommunity structure, as has been proposed previously (Dallas et al., 2016).

Differences in metacommunity structures between macroinvertebrates and diatoms

Our second hypothesis (**H_2**) assumed that diatoms with high passive dispersal capability should be more able to track environmental heterogeneity along the environmental gradients compared with macroinvertebrates, and diatoms should thus show stronger environmental filtering than macroinvertebrates (Astorga et al., 2012). However, contrary to our hypothesis, diatoms exhibited more random distributions than macroinvertebrates in the QTR and MKR regions, while macroinvertebrates showed more Clementsian structures than diatoms. This finding suggests that environmental filtering was stronger for macroinvertebrates than for diatoms. There are at least two potential explanations for these findings. First, aquatic insects were the dominant taxa among the macroinvertebrates (these comprised 93%, 87%, and 92% collected taxa in the ITR, QTR, and MKR regions, respectively) and can often actively select suitable habitats for dispersal (Heino, 2013). Therefore, macroinvertebrates may be able to track environmental variation well through the active dispersal and show stronger environmental filtering than diatoms, which are passively randomly dispersed by wind, stream flow and animals (Kristiansen, 1996). Second, unlike a large-scale study covering multiple drainage basins (Astorga et al., 2012), we studied metacommunities within drainage basins, where actively-dispersing insects probably can select suitable habitats better than diatoms (Heino, 2013). Similarly, previous studies have also found evidence that the degree of environmental filtering was weaker for diatoms compared with macroinvertebrates in streams at a within-basin scale (Heino et al. 2012).

Consistent with previous stream studies (Heino et al., 2012; Heino, Nokela, et al., 2015), our results imply that the underlying important environmental drivers in metacommunity structure are context dependent. Typically, diatom taxa replaced one another in discrete communities (i.e. Clementsian view) or in a continuum of communities (i.e. Gleasonian view) across the elevation and mean diurnal range gradient (Appendix S4). These results suggest that elevation and mean diurnal range temperature were highly important to the structure of diatom communities, while other environmental variables such as water temperature, total dissolved solids, and forest cover were also strongly important for macroinvertebrate communities. However, the relative importance of these environmental drivers varied among the region. For example, when site-by-taxa matrix was ordered

by forest cover, Clementsian structures were present in the QTR regions, whereas random patterns were present in the ITR region (Appendix S4). This indicates that land-use diversity was highly important for the structure of macroinvertebrate assemblages in the QTR regions (Wang et al., 2012), but it was not important for these assemblages in the ITR region.

Variation in metacommunity structures among taxonomic levels

We further hypothesized ($\mathbf{H_3}$) that turnover-driven patterns should be more typical at lower taxonomic levels. This hypothesis was partially supported, as the likelihood of Clementsian structure was higher at the lower taxonomic levels (i.e. species), but only for diatoms in the MKR and QTR regions. However, Gleasonian and Q-Gleasonian structures occurred only at higher taxonomic levels (family and genus) for diatoms (Table S4.1), suggesting that different taxonomic levels in diatoms may respond differently to the same environmental gradients. A potential underlying reason may be that families and genera have broader distributions than species, which would result in more overlap in distributions. This should, in turn, lead to Gleasonian structures (Cisneros, Fagan, & Willig, 2015). While the patterns differed among taxonomic levels in diatoms, idealized metacommunity structures were highly similar between genus- and family-level data sets of macroinvertebrates, except in the taxa-rich region (i.e. MKR region, Appendix S5). Such difference might be related to different numbers of species or genera within genera or families between diatoms and macroinvertebrates. The number of species within genera and families were relatively high in diatoms, while the number of genera within families were relatively low in macroinvertebrates (Appendix S5). Typically, when diversity at the species level is high, species within genera have undergone adaptive radiation, with species showing different environmental responses within genera or families (Heino & Soininen, 2007). Thus, it is not surprising that diatoms show weaker congruence in metacommunity structure across taxonomic levels than macroinvertebrates. Our results suggest that, for macroinvertebrates, family-level data could be used as surrogates for genus-level patterns in metacommunity. However, one important limitation in our study is that we could not use species-level data for macroinvertebrates because we were unable to identify macroinvertebrates to species level. A future challenge of macroinvertebrate metacommunity studies is to incorporate comprehensive species-level data (e.g. through DNA barcoding), at least in China.

Table 1: Summary of the basic information about the three study basins.

	Irtysh River (ITR)	Middle Qiantang River (QTR)	Mekong River (MKR)
Region's midpoint	48° N, 88° E	29° N,119° E	22° N, 101° E
Annual precipitation	232 mm	1,558 mm	1,610 mm
Annual mean temperature	4°C	17°C	21°C
Spatial extent	311 km	206 km	168 km
Climate type	Temperate arid climate	Subtropical monsoon climate	Tropical monsoon climate
Land use characteristics	Cattle grazing; natural forest; some metal mining	Aggregated mining; agricultural practice; urban development	Artificial forest plantations; agricultural practice; urban development

Figure 1: Geographic locations of the sampling sites in three regions: the upper section of the Mekong River (MKR) in Xishuangbanna prefecture, the middle section of Qiantang River (QTR) in Zhejiang Province, and the Irtysh River (ITR) in Xijiang autonomous region.

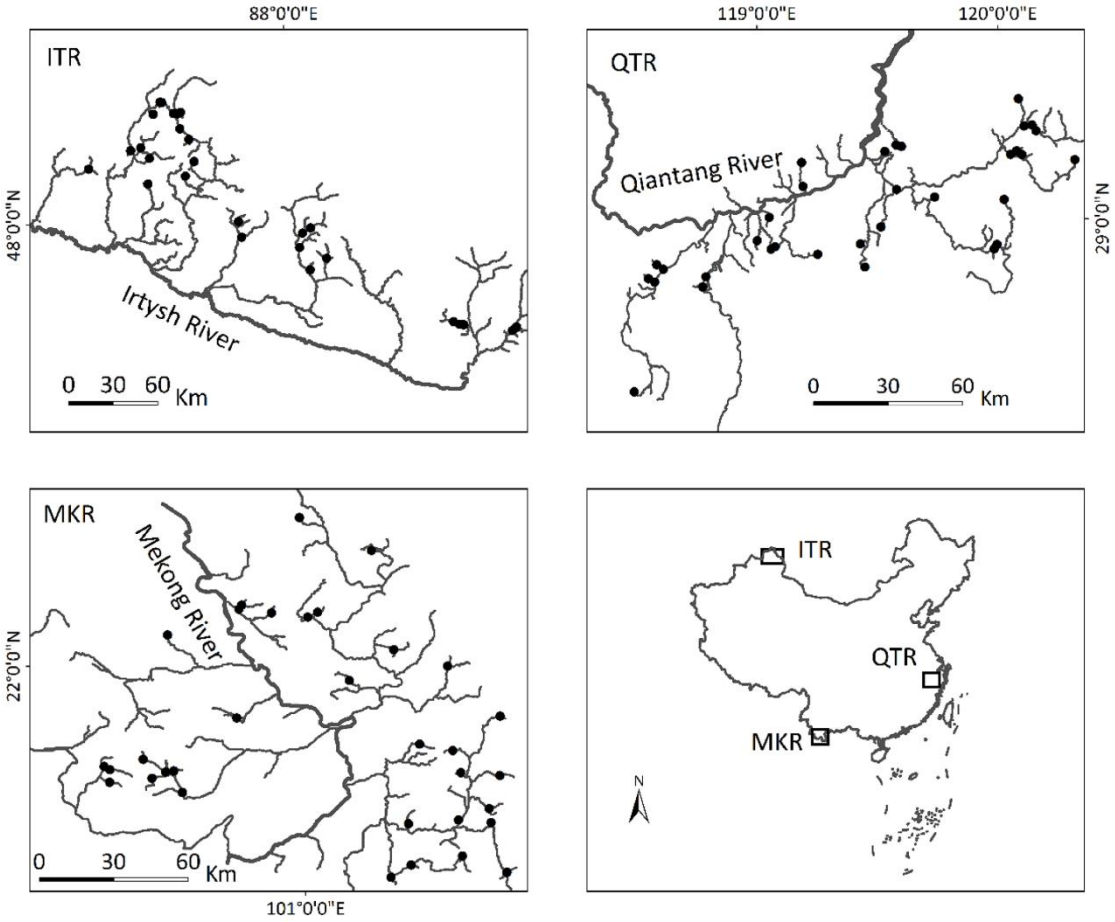
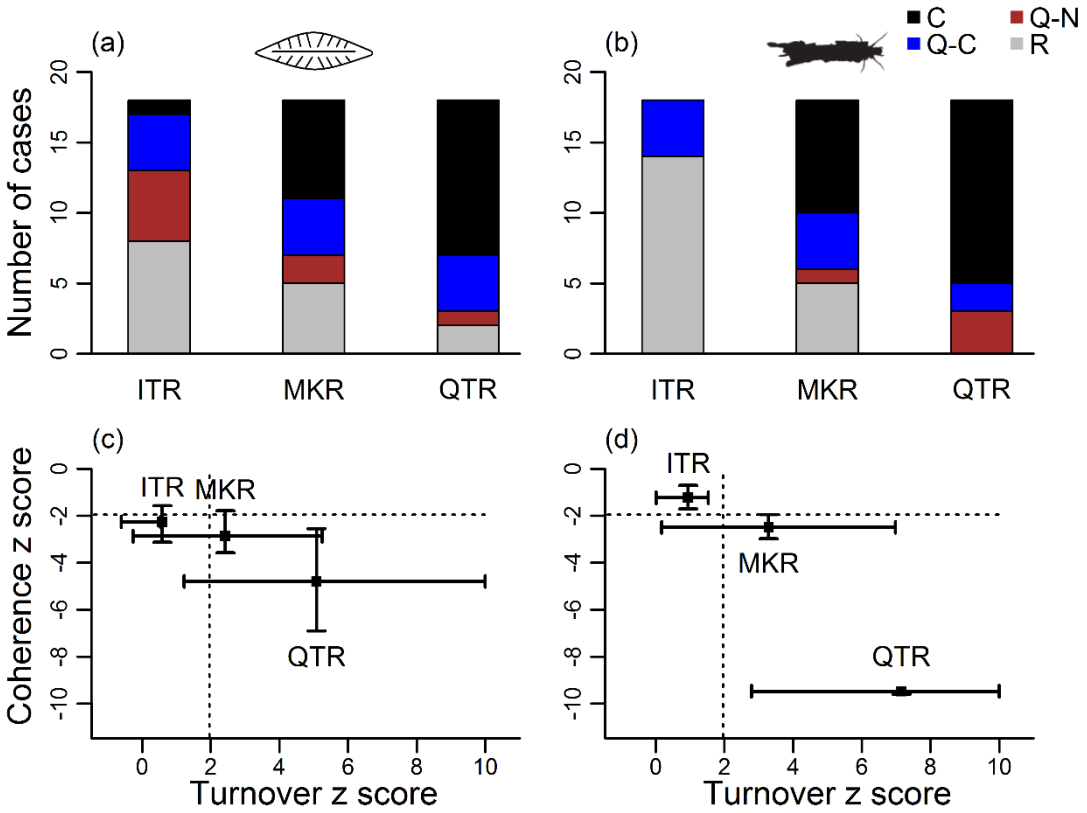


Figure 2: Metacommunity structures (a and b) and mean coherence z score vs. mean turnover z score (c and d) detected by the elements of metacommunity structure analysis for diatoms and macroinvertebrates in three regions: the upper section of the Mekong River (MKR) in Xishuangbanna prefecture, the middle section of Qiantang River (QTR) in Zhejiang Province, and the Irtysh River (ITR) in Xijiang autonomous region (see text for the details of z score calculation). Analyses were conducted for diatoms at species levels (a and c), and for macroinvertebrates at genus levels (b and d). The metacommunity structures are Clementsian C, Quasi-Clementsian Q-C, Quasi-Nested Q-N, and Random R. The total number of analysed matrices was 18 per region and per taxonomic group. Point represents the mean; upper and right bar represent the 75% quantiles; lower and left bar represent the 25% quantiles. Coherence z scores below -10 are converted to -10. Turnover z scores above 10 are converted to 10. The dashed lines indicate the coherence z score = -1.96 and the turnover z score = 1.96.



Data accessibility: The data will be deposited to Dryad if the paper is accepted for publication.

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Biosketch: Siwen He is a PhD student interested in the environmental and spatial factors influencing metacommunity structures in streams. Author contributions: S. H., B. W. and J. S. conceived the ideas, S. H. analysed the data, K. C., B. W. and N. D. collected the field samples, S. H., J. S. and J. H. led the writing, and all authors contributed to the writing of the paper.